

Intertidal zonation patterns of macroinfauna over a range of exposed sandy beaches in south-central Chile

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ABSTRACT: Ten sandy beaches, covering a range from reflective to dissipative conditions, were sampled in south-central Chile to determine whether different beach morphodynamic states support different macroinfaunal zonation patterns. Three patterns were distinguished through examination of kite diagrams and analysis using multivariate techniques: (1) in reflective beaches with coarse sand, a single zone of air-breathing crustaceans was located above the drift line; (2) a reflective beach with finer sands exhibited 2 faunal zones due to the addition of a second zone of cirrolanid isopods below the drift line; and (3) in intermediate and dissipative beaches 3 faunal zones were delineated, the above 2 plus a broad zone covering the lower shore. Species representative of these zones are *Orchestoidea tuberculata* and *Excirolana braziliensis* in the upper shore, *E. hirsuticauda* and *E. monodi* in the middle shore and *Emerita analoga* and *Bathyporeia pus magellanicus* in the lower shore. This study also showed that zones were ordinated along an intertidal gradient of sediment water content. The 3 zone pattern agrees with the worldwide scheme proposed by Dahl (1952; Oikos 4: 1–27). Body-size comparisons showed that individual sizes in some species differed across their intertidal distribution.

INTRODUCTION

Several attempts have been made to construct zonation schemes for sandy beach macroinfauna, either for worldwide application, or at least for littoral areas over wide latitudinal ranges. Dahl (1952), Pichon (1967) and Trevallion et al. (1970) based their schemes on the presence of particular belts or assemblages of invertebrates. Dahl (1952) used crustaceans from European and South American sandy beaches to produce one of the most comprehensive schemes to date. He proposed 3 zones: a higher zone (the subterrestrial fringe), occupied either by talitrid amphipods or ocypodid crabs; a middle zone (the midlittoral zone) with cirrolanid isopods as the main constituent, and a lower zone (the sublittoral zone) in which haustoriid and oedicerotid amphipods, hippid crabs (*Emerita* spp.), molluscs and polychaetes are found. Salvat (1964, 1966, 1967) proposed 4 physical zones for sandy beaches: drying, retention, resurgence and saturation zones, each zone

characterized by an increasing water content. Many subsequent studies have reported and debated similarities and differences between these schemes (e.g. Gauld & Buchanan 1956, Wade 1967, Jones 1971, Epelde-Aguirre & Lopez 1975, Jaramillo 1978, 1987b, Raffaelli et al. 1991, De Ruyck et al. 1992).

In most cases the zonation of the macroinfauna has been analyzed without taking into account physical differences between beaches. This is surprising considering the physically controlled nature of communities on exposed beaches. However, a few studies have shown that morphodynamic variability among beach types may account for differences in zonation. For example, Trevallion et al. (1970) suggested that many differences observed among tropical beaches (e.g. species richness) were related to differences in exposure and beach slope. Gauld & Buchanan (1956) and Dye et al. (1981), working on tropical and subtropical beaches, and McLachlan (1985) and Jaramillo & González (1991) examining temperate sandy beaches,

have related differences in the composition of the macroinfauna to differences in beach morphology.

Exposed sandy beaches can be classified into 3 general morphodynamic types: reflective, intermediate and dissipative (Short 1979, Wright & Short 1983, Wright et al. 1985). On reflective beaches, breakers surge and collapse close to the base of the beach face, which reflects much of the incident-wave energy. Such beaches have steep profiles and usually coarse sand grains. In contrast, dissipative beaches have a wide, multibarred surf zone; waves break far seaward of the beach face and dissipate most of their energy before reaching the beach. They have flatter profiles, and usually fine-grained sands. Intermediate beaches have intermediate profiles, fine to medium sands, and intermediate surf zones characterized by bars, troughs and rip currents (Short 1979, Wright & Short 1983). This categorization is thus based upon the interaction between wave energy, sediment particle size and sediment abundance (Short & Hesp 1982, Wright & Short 1984).

Recent studies carried out on beaches in South Africa, Australia, the west coast of the USA and south-central Chile (McLachlan 1990, McLachlan et al. 1993, Jaramillo & McLachlan in press) have shown that beach type, which can be defined by Dean's parameter (Wright & Short 1983), is a good predictor of species richness, abundance and biomass of the macroinfauna; i.e. in general these community parameters increase towards dissipative conditions. Swash characteristics (e.g. swash period, number of effluent line crossings) that are distinctive for each type of beach (McArdle & McLachlan 1991, 1992) may also influence the community structure of the macroinfauna.

In view of the above, we hypothesized that over a short latitudinal range the zonation patterns of the macroinfauna would differ only in response to changes in beach type, since zoogeographic variability would be excluded. To test this hypothesis, we examined the intertidal zonation of the macroinfauna over a range of conditions from reflective to dissipative of sandy beaches in south-central Chile. We also investigated the intertidal zonation of the most representative species to examine their responses to different beach conditions.

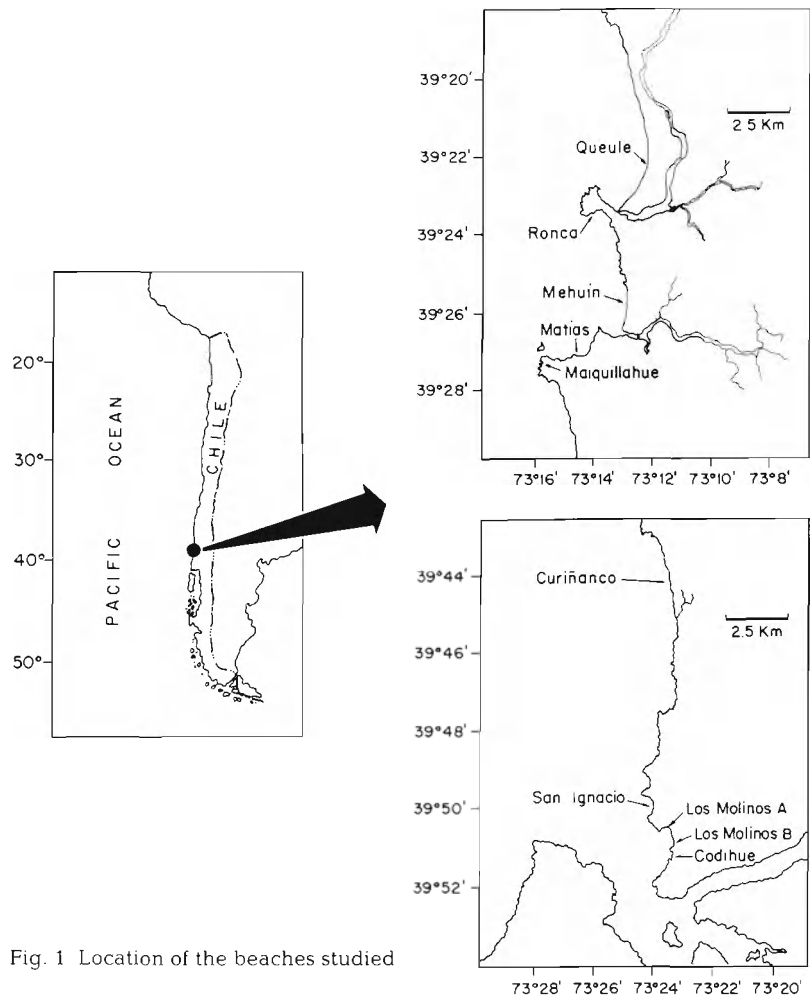


Fig. 1 Location of the beaches studied

MATERIALS AND METHODS

Study area. The 10 beaches studied were located in the south-central area of the Chilean coast (approximately 39 to 40° S, Fig. 1) and were selected to illustrate different morphodynamic stages. Maquillahue, Codihue and Los Molinos A had reflective characteristics; Los Molinos B, San Ignacio, Matías, Curiñanco and Queule were intermediate beaches, while Mehuín and Ronca displayed dissipative features (Jaramillo & McLachlan in press). All the sites were fully exposed to the breaking waves of the Pacific Ocean. Most beaches were near estuarine areas, but none were located within 500 m of estuaries; thus surf salinities along the beaches studied range approximately from 25 to 32‰. The range for water temperature is ca 10 to 16°C, and the tides are semidiurnal with a maximum range of 1.5 m.

Sampling and analytical procedures. The beaches were sampled once during the spring low tides of

March 1991. A transect was extended from above the drift line to below the swash line on each beach, and 10 equally spaced sampling stations were marked: the uppermost above the drift line, the second on the drift line and the last in the swash zone. At each station four 0.03 m² replicates (1 m apart) were taken with plastic cylinders to a depth of 30 cm and sieved through 1 mm mesh sieves. The residue in the sieves was preserved in 5 % formalin; the animals were later sorted from the sediments, identified and counted. The most abundant species were measured to the nearest 0.1 mm length to evaluate zonation by size. These were the talitrid amphipod *Orchestoidea tuberculata* Nicolet, the cirrolanid isopods *Excirrolana braziliensis* Richardson and *E. hirsuticauda* Menzies and the anomuran crab *Emerita analoga* (Stimpson). For the amphipods, body length was defined as the distance from rostrum tip to telson base, whereas in the isopods, body length was defined as the distance from rostrum tip to telson tip. The cephalothorax length of *E. analoga* was used as a measure of body size.

The morphology (i.e. beach face slope) of each site was determined by Emery's profiling technique (Emery 1961). The slope of each station was measured

with a clinometer (4 readings). Two replicate samples of sediment for grain size analyses were collected at each station by inserting a 3.5 cm diameter metal core to a depth of 10 cm. Samples were wrapped in aluminium foil and weighed soon after collection. Holes were excavated at each station to measure the depth of the water table. The penetrability of the sediments was measured by dropping a 33.6 g metal rod down a 1 m tube. The depth to which the rod penetrated into the sediment was measured 4 times at each station.

Grain size was analyzed by settling tube (Emery 1938), and mean grain size was calculated according to the moments computational method (Seward-Thompson & Hails 1973). The water content of the sand was estimated as the loss in weight of wet sediments after drying (120 °C for 96 h).

Variability in the physical characteristics (slope, mean grain size, water content of the sediment, depth of water table and penetrability of sands) of stations at each beach was analyzed by Principal Component Analysis (PCA; STATGRAPHIC statistical package). Density values per m² were calculated and used to draw kite diagrams to describe zonation patterns. To analyse the zonation of species at each beach, macro-

infaunal samples were subjected to 3 multivariate techniques: (1) numerical classification analysis was used to illustrate the similarity between sampling stations. Dendrograms were constructed from Bray-Curtis similarity matrices, based on a group-average sorting strategy (Field et al. 1982), using the BIOSTAT statistical package (Pimentel & Smith 1985); (2) ordination of samples was performed by Non-metric Multi-dimensional Scaling (NMDS) of the Bray-Curtis similarity matrices (BIOSTAT statistical package; Pimentel & Smith 1985); and (3) Canonical Correspondence Analysis (CCA) of species data was used to establish the relationships between sampling stations, species and environmental factors (CANOCO statistical program; Ter Braak 1987). All these multivariate analyses were performed on root-root transformed data (Field et al. 1982). Stations where no species were present were excluded from the analyses.

RESULTS

Beaches

Textural characteristics and beach face slopes showed high variability between sites. The coarsest particles (<1 Φ) were found at Maiquillahue and Codihue, the beaches with the steepest slopes (Fig. 2). In general, the beaches with the finest sands (Ronca, Matías,

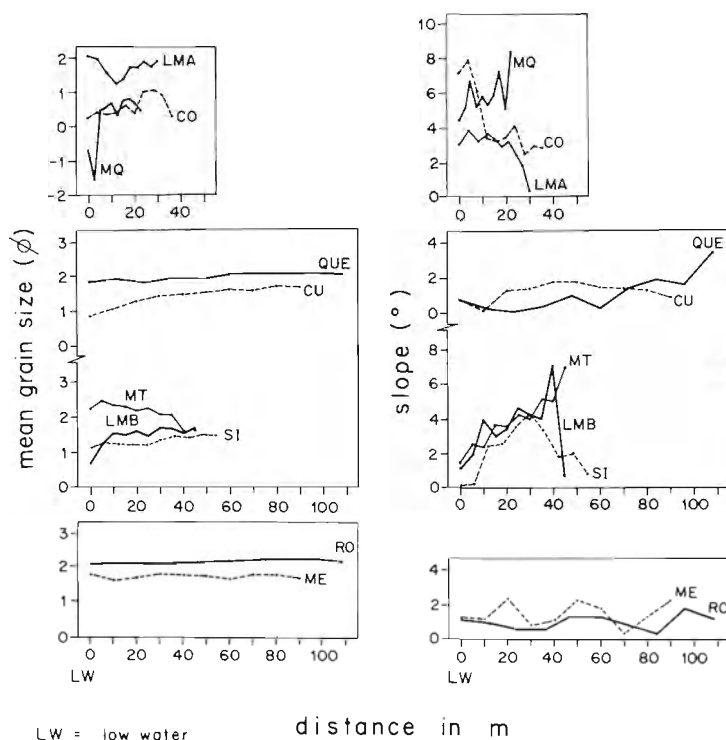


Fig. 2. Intertidal variability in mean grain size and beach face slope across the stations sampled at the reflective beaches at Maiquillahue (MQ), Codihue (CO) and Los Molinos A (LMA), at the intermediate sites at Los Molinos B (LMB), San Ignacio (SI), Matías (MT), Curiñanco (CU) and Queule (QUE), and at the beaches with dissipative characteristics, Mehuin (ME) and Ronca (RO). Distance is from the low water mark (the lowest station from each transect)

Queule and Mehuín) had flattest slopes. Based on the overall mean grain size values, Maiquillahue and Codihue had coarse sands, and Matías and Ronca fine-grained sands, whereas all the others had medium-grained sands. The reflective beaches at Maiquillahue and Codihue displayed coarsest grains in the lower intertidal, whereas limited variability in sand particle size was found across the intertidal zones of the other beaches.

Depth of the water table increased towards the upper shore as the water content of the sediments decreased (Fig. 3). The deepest water table was found 158 to 175 cm below the surface in the upper stations of the reflective beach at Codihue. Deep water tables were also observed in the reflective beach at Maiquillahue (135 to 140 cm below the surface) and at the intermediate site at Los Molinos B (138 to 140 cm below the surface). The depth of the water table in the other beaches ranged from 60 to 124 cm below the surface at the upper stations, Mehuín being the beach with the shallowest water table at those levels (56 to 77 cm below surface).

Sand water-content percentages as high as 24 to 26% were measured in the lower stations of beaches with intermediate and dissipative characteristics. In contrast, for beaches with the most reflective characteristics (Maiquillahue and Codihue) the highest water-content values only reached 13 to 15%. Water-content changes across the intertidal zone were more

gradual below the drift lines of beaches tending towards dissipative conditions (Queule, Mehuín and Ronca) (Fig. 3). The penetrability of the sediments tended to decrease from upper to lower shore stations, with the exception of Maiquillahue where the highest values were measured at high and low intertidal stations, and Codihue where the lowest stations had the highest penetrability (Fig. 3).

Fig. 4 shows the results of ordination of stations by PCA using the physical characteristics of the beaches. The first 2 components accounted for 82.6 to 100 % of the total variance, and the bulk of this variance was explained by the first component (55.9 to 99.2 %). Water table and water content had the highest loadings in the first component, while slope and mean grain size loaded highest in the second. The exception to this trend was Maiquillahue where mean grain size also had a high loading in the first component, whereas penetrability had the highest loading in the second component. The distribution of station-points along the axis representing the first component tended to be gradual in most plots. However, upper beach levels (either Stn 1 or Stns 1 & 2, above or at the drift line) were often separated from the other ones. Further, stations located on the lower shore (Stns 9 & 10) separated quite well from those of the middle shore in the reflective beaches at Maiquillahue and Codihue, and in the intermediate sites at Los Molinos B and Curiñanco (Fig. 4).

Macroinfauna

The highest number of species (14) was found at Ronca, the most dissipative beach, while the lowest number occurred at the coarse-grained reflective beaches at Maiquillahue and Codihue where the talitrid amphipod *Orchestoidea tuberculata* was the only species collected (Fig. 5). The highest abundances were registered in the intermediate beaches at Matías and Curiñanco (53 706 and 66 783 ind. m⁻¹ respectively) and in the dissipative beach at Ronca (41 654 ind. m⁻¹). Apart from Maiquillahue and Codihue, the cirrolanid isopod *Excirolana hirsuticauda* was the species with the highest abundance at all the other beaches apart from San Ignacio where *O. tuberculata* ranked first (Figs. 6 & 7).

No classification or NMDS ordination could be performed for beaches at Maiquillahue and Codihue because *Orchestoidea tuberculata* was the only

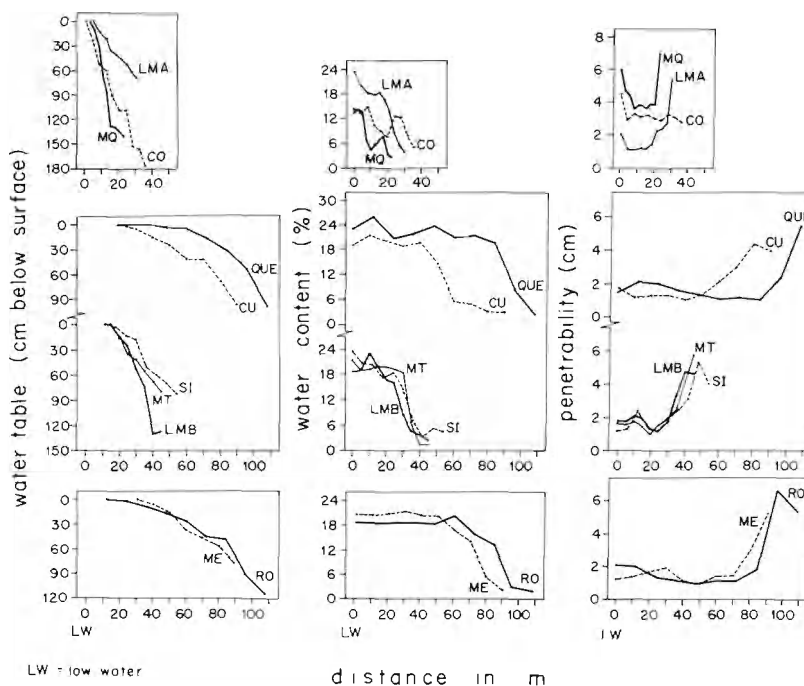


Fig. 3. Intertidal variability in depth of water table, water content and penetrability of the sediments at the stations sampled. Codes for beaches as in Fig. 2

species collected. This species was collected at the 2 highest stations at Los Molinos A where most of the intertidal was dominated by *Excirolana hirsuticauda*. Two station groupings were delineated in the cluster analysis and NMDS ordination for Los Molinos A: one with the 2 uppermost stations (inhabited by *O. tuberculata*) and another with the rest of the stations (dominated by *E. hirsuticauda*). Thus, 2 faunal zones were differentiated in this medium-grained reflective beach (Fig. 5).

The down-shore distribution of the macroinfauna in the beaches with intermediate characteristics exhibited greater complexity (Fig. 6). In general, the results of classification and NMDS ordination analyses rendered similar results. Three faunal zones were discernible in all 5 beaches, but with varying degrees of clarity. The upper zone was characterized by *Orchestoidea tuberculata* and the cirrallid isopod *Excirolana braziliensis*; the middle zone had *E. hirsuticauda* as the dominant species, but also the spionid polychaete *Euzonus heterocirrus* and occasionally *Emerita analoga*; the lower zone was the most diverse with *E. analoga*, the polychaete *Nephtys impressa*, the isopods *Macrochiridothea setifer* and *Chaetilia paucidens*, the amphipods *Bathyporeiapus magellanicus*, *Phoxocephalopsis mehuinensis*, *Tryphosella schellenbergi*, *Huarpe* sp. and *Ampelisca* sp. and juveniles of the bivalve *Mesodesma donacium* (Fig. 6).

Mehuín and Ronca, the beaches with the most dissipative characteristics, displayed a similar zonation pattern to that shown by the intermediate beaches (Fig. 7), i.e. 3 zones characterized by the same species mentioned above. The zonation was more distinct in these 2 beaches than in the intermediate beaches which had less clear separation of zones.

Dominant patterns in community composition in relation to the environmental variables beach face slope, mean grain size and water content are displayed in the CCA ordination diagrams (Figs. 8, 9 & 10). The total variance of the species data explained by the first 2 ordination axes was 57.2, 20.5 and 24.3 % for the reflective, intermediate and dissipative groups of beaches

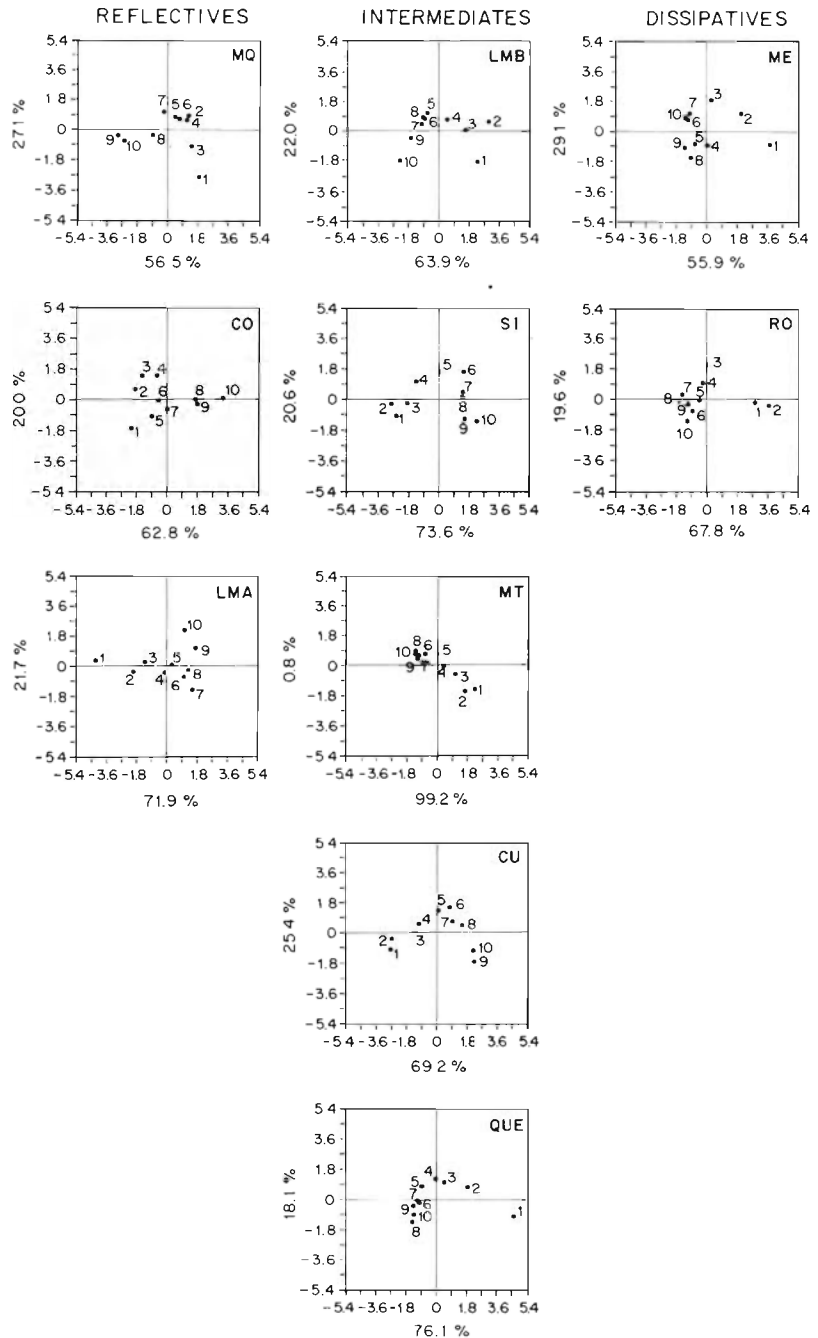


Fig. 4. Ordination of stations sampled at each beach based upon principal component analysis. Codes for beaches as in Fig. 2

respectively. The total variance of these 2 axes explained by the environmental variables ranged from 89 to 100 % for the 3 groups of beaches. Two environmental factors, depth of water table and penetrability of sands, were excluded from the CCA because multicollinearity among them indicated that they made no unique contribution to the regression (Ter Braak 1987) and water content was deemed more accurate and relevant. Penetrability and depth of water table were sig-

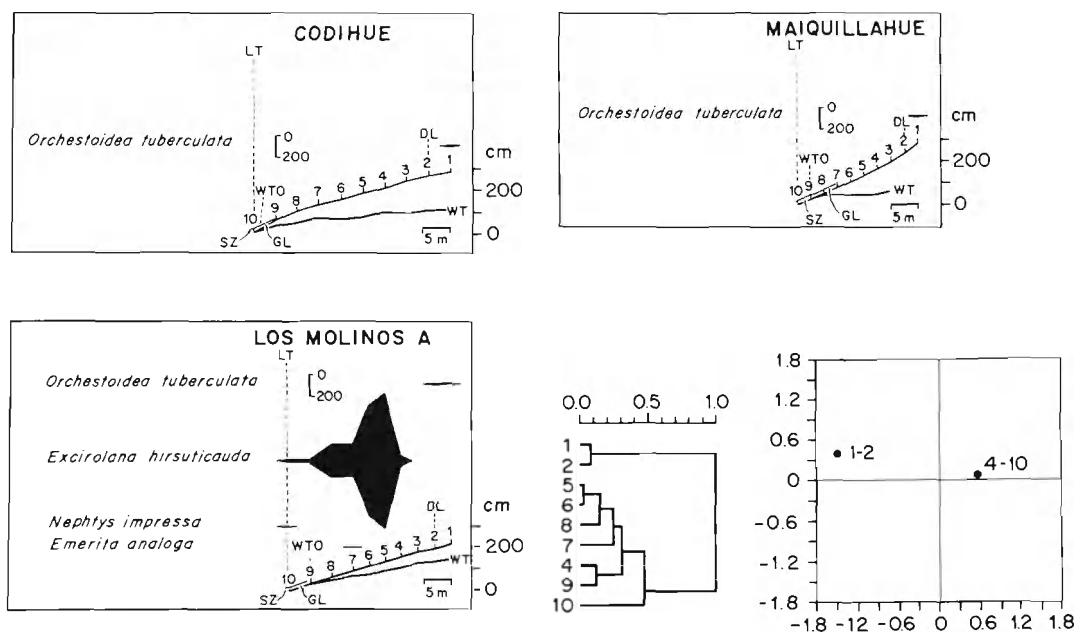


Fig. 5. Intertidal distribution of the macroinfauna, and clustering and ordination (Non-metric Multi-dimensional Scaling) of stations at 3 beaches with reflective characteristics. Beaches with a single species were omitted from classification and ordination analyses whereas stations without any species were omitted from cluster diagrams. SZ: surf zone; WT: water table; WTO: water table outcrop; GL: glassy layer; DL: drift line

nificantly correlated ($p < 0.05$, Spearman's rank correlation) with water content in all 3 beach types.

The environmental factors were significantly ($p = 0.01$; Monte Carlo permutation test) correlated with the first ordination axis of the CCA (Figs. 8, 9 & 10). Water content was significantly correlated to Axis I and was the most important environmental variable. It contributed 93.6, 66.3 and 82.9% to the total variance explained by all the variables for reflective, intermediate and dissipative beach types respectively. Beach face slope and mean grain size were of little importance as environmental variables. If the effects of water content are eliminated from the CCA by treating it as a covariable during the extraction of ordination axes, the other environmental variables show no meaningful trends in the ordination.

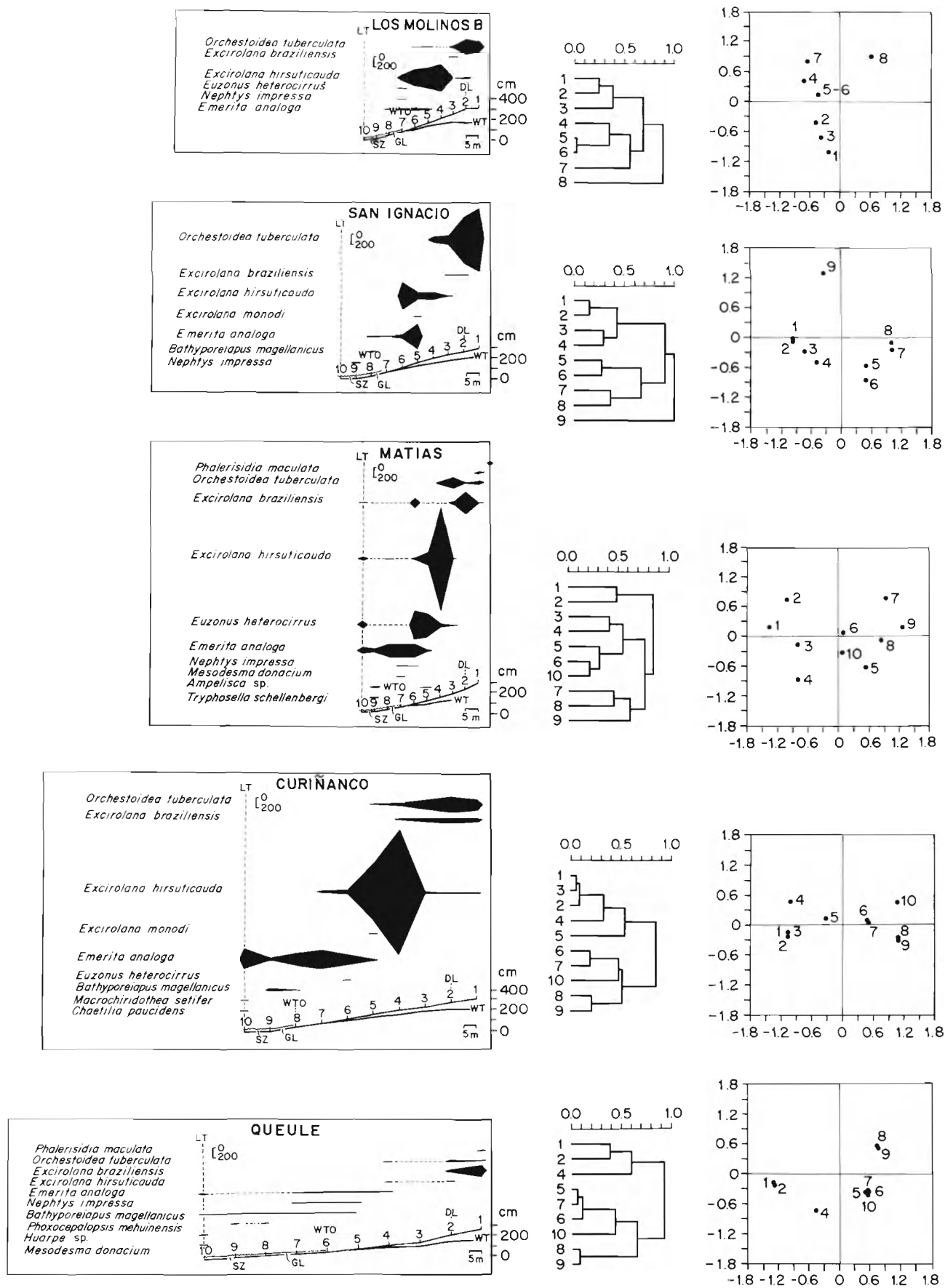
For all 3 beach types most sites were ordinated along the first ordination axis (Figs. 8, 9 & 10), indicating a change in community structure along the vertical aspect, i.e. intertidal gradient of the beaches. Upper shore stations were positively correlated with a low water content of the sand and vice versa. The ordination for reflective beaches indicates a distinct separation between upper and middle shore stations, whereas in dissipative beaches 3 zones can be distinguished. All 3 zones are represented in the CCA of intermediate beaches, although the middle and lower shore zones show a greater overlap (Figs. 8, 9 & 10).

The species were broadly ordinated along the first axis (Figs. 8, 9 & 10), showing a clear association with a change in water content along the intertidal zone of all beaches. The distribution patterns of the more common species along the down-shore gradient were similar to those illustrated in Figs. 5, 6 & 7. Rare and less abundant species (e.g. *Chaetilia paucidens*, *Macrochiridothea setifer*, *Thyphosella schellenbergi* and *Ampelisca* sp.) were placed at the extreme edges of the ordination diagrams and thus were of little importance (Ter Braak 1987).

Table 1 shows body-size variability of the most representative species across the intertidal in different types of beaches. Body sizes of *Orchestoidea tuberculata* and *Excirolana braziliensis* were generally not significantly different between tidal levels in Curiñanco and Ronca beaches. *E. hirsuticauda* tended to be larger in the central zones of its distribution at Los Molinos A, Curiñanco and Ronca. Finally, the body size of *Emerita analoga* was greater at the lower intertidal levels sampled in the 2 beaches compared (Table 1).

DISCUSSION

It was hypothesized that different beach types in south-central Chile might harbour different intertidal macroinfauna zonation patterns. Our results support



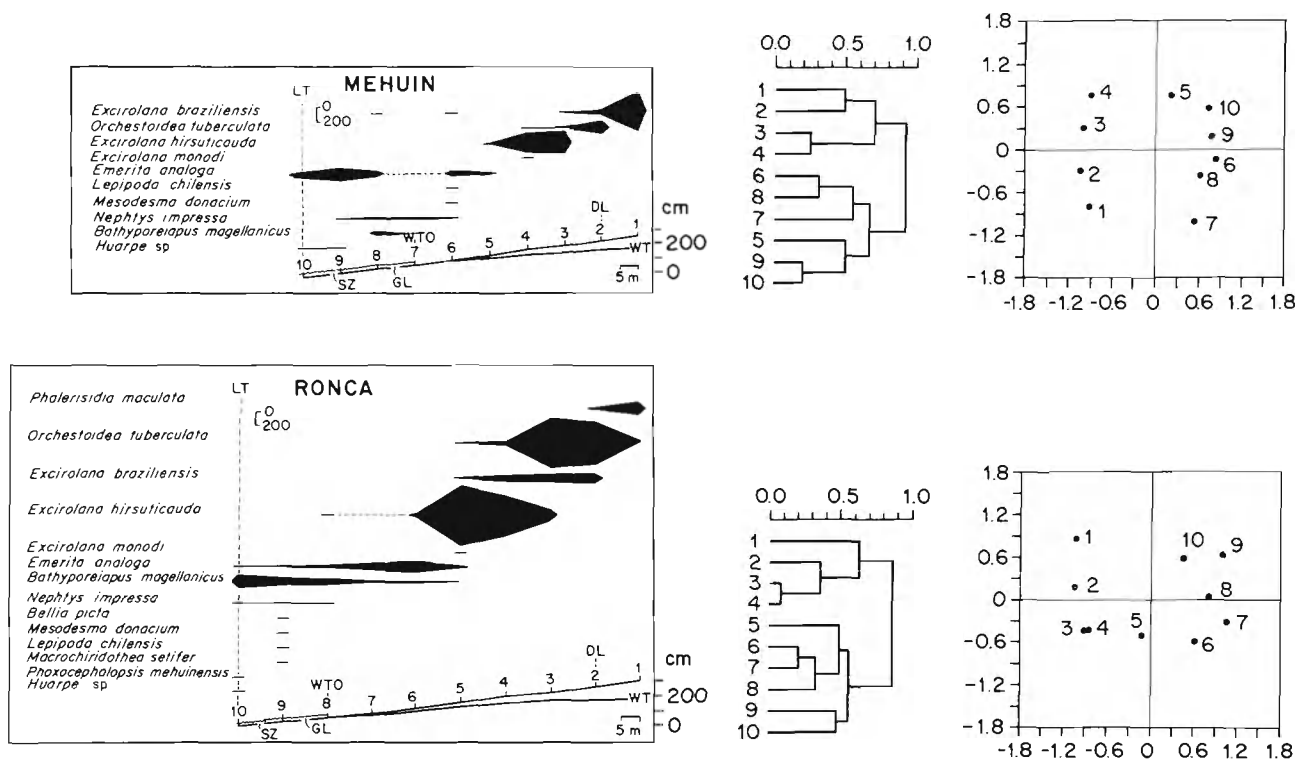


Fig. 7. Intertidal distribution of the macroinfauna, and clustering and ordination of stations at 2 beaches with dissipative characteristics

this hypothesis since we were able to recognize 3 scenarios over 10 beaches in a limited latitudinal range. These results show that morphodynamic variability in beach types must be taken into account when macroinfaunal zonation is discussed. McArdle & McLachlan (1991, 1992) showed that swash climates are quite distinctive in reflective, intermediate and dissipative beaches and communities may respond to this (McLachlan et al. 1993). Thus, studies including just one beach or even several belonging to the same morphodynamic states (e.g. Bally 1983, Wendt & McLachlan 1985, Clarke & Peña 1988, Raffaelli et al. 1991) may not lead to findings relevant to other beach types. This is the first study to compare zonation patterns over a range of reflective to dissipative conditions.

Distinct zonation characterized the intermediate and dissipative beaches, and included 3 faunal zones: an upper zone with talitrid amphipods and a cirrolanid isopod (*Excirolana braziliensis*), a middle zone dominated by *E. hirsuticauda* and where spionid polychaetes and occasionally the anomuran *Emerita analoga* were also found; and a lower zone dominated by *Emerita analoga* and characterized by organisms such as amphipods, isopods and brachyurans that are also found in the surf zone (Jaramillo 1982). Examination of the kite diagrams and the results of the classification and ordi-

nation analyses (especially for the beaches at Mehuín and Ronca), showed that the lowest zone was the least sharply defined.

The lower zone of the intermediate and dissipative beaches supported the greatest number of species, a characteristic also found for the lower shore of dissipative sandy beaches in the USA (McLachlan 1990) and South Africa (Bally 1983, Wendt & McLachlan 1985). This zone was also wider in the beaches at Mehuín and Ronca, the most dissipative sites. Visual observations confirmed that this lower zone included the resurgence and saturation zones proposed by Salvat (1964, 1967). It appears that the swash climate in dissipative beaches enables species such as *Emerita analoga* to move throughout the swash and surf zones, resulting in a single faunal zone.

A variation on this 3-zone scheme is the zonation which characterized the fully reflective beaches at Maiquillahue and Codihue where the macroinfauna was represented only by the talitrid amphipod *Orchestoidea tuberculata* living above the high-water mark or drift line. The absence of this species from the intertidal of these beaches cannot be related to the general trend of increasing grain size towards the lower shore. This assertion is supported by field studies that have shown that this amphipod is able to burrow in sands as coarse as those present in these beaches, pro-

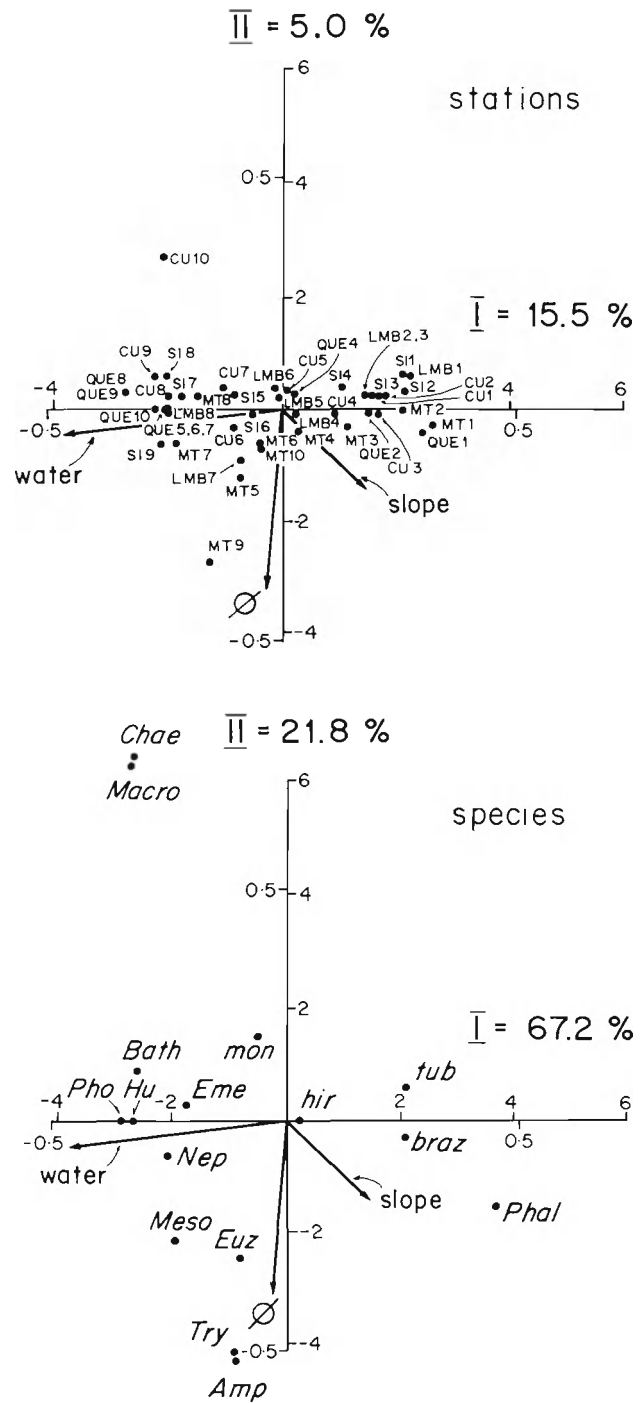


Fig. 9. Intermediate beaches. Ordination biplots obtained from Canonical Correspondence Analysis of stations, species and environmental variables. LMB: Los Molinos B; SI: San Ignacio; MT: Matías; CU: Curiñanco; QUE: Queule. *phal*: *Phalerisidia maculata*; *tub*: *Orchestoidea tuberculata*; *braz*: *Excirolana braziliensis*; *hir*: *Excirolana hirsuticauda*; *Mon*: *Excirolana monodi*; *Euz*: *Euzonus heterocirrus*; *Eme*: *Emerita analoga*; *Nep*: *Nephtys impressa*; *Bath*: *Bathyporeia pus magellanicus*; *Pho*: *Phoxocephalopsis mehuinensis*; *Hu*: *Huarpe* sp.; *Meso*: *Mesodesma donacium*; *Amp*: *Ampelisca* sp.; *Try*: *Tryphosella schellenbergi*; *Macro*: *Macricheiridothea setifer*; *Chae*: *Chaetilia paucidens*

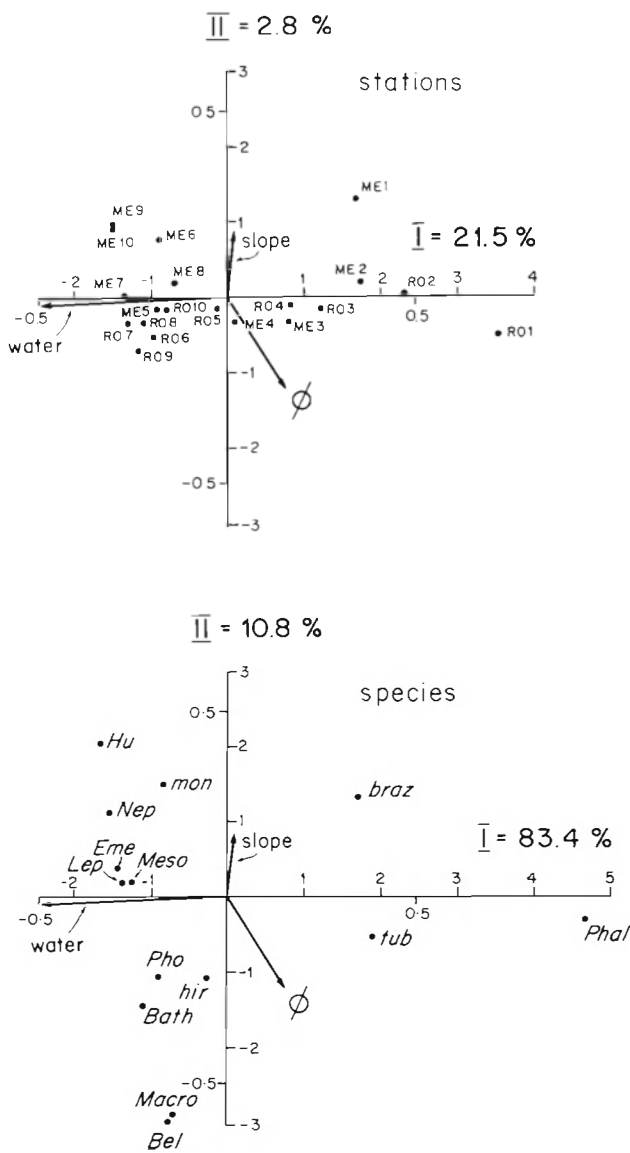


Fig. 10. Dissipative beaches. Ordination biplots obtained from Canonical Correspondence Analysis of stations, species and environmental variables. ME: Mehuin; RO: Ronca. *phal*: *Phalerisidia maculata*; *tub*: *Orchestoidea tuberculata*; *braz*: *Excirolana braziliensis*; *hir*: *Excirolana hirsuticauda*; *Mon*: *Excirolana monodi*; *Eme*: *Emerita analoga*; *Bath*: *Bathyporeiapus magellanicus*; *Nep*: *Nephtys impressa*; *Bel*: *Bellia picta*; *Meso*: *Mesodesma donacium*; *Lep*: *Lepidopa chilensis*; *Macro*: *Macrlichiridothea setifer*; *Pho*: *Phoxocephalopsis mehuinensis*; *Hu*: *Huarpe* sp.

beaches the harsh swash climate excludes the establishment of intertidal macrofaunal species. McLachlan (1985) found that a talitrid amphipod was the only important macrofauna species living in a reflective beach of Australia, while at another reflective site no macrofauna was found at all. Gauld & Buchanan (1956) and Dye et al. (1981) also reported the absence

Table 1. Body-size comparison among stations at which the most abundant species were collected. Values are means (mm), with standard deviation in parentheses. Means connected by lines are not significantly different at the 0.05 probability level (1-way analysis of variance and Tukey-Kramer multiple comparison test)

	Los Molinos A				Curianco				Ronca			
	Stn 4	Stn 5	Stn 6	Stn 7	Stn 8	Stn 9	Stn 10	Stn 11	Stn 1	Stn 2	Stn 3	Stn 4
<i>Orchestoidea tuberculata</i>	5.9(2.2)	7.5(1.7)	6.4(2.0)	7.6(2.4)	7.4(1.9)	6.3(1.3)			7.6(7.2)	8.0(4.5)	10.6(5.4)	
<i>Excirolana braziliensis</i>									6.2(1.7)	6.6(2.1)	6.7((2.0)	
<i>Excirolana hirsuticauda</i>									5.9(1.3)	5.9(1.5)	6.7(2.0)	
<i>Emerita analoga</i>									11.1(0.7)	9.0(3.4)	12.8(3.6)	18.9(3.0)

of macroinfauna in the intertidal zones of beaches with reflective conditions in Ghana and Natal respectively.

Another variation on the 3-zone scheme was the zonation found at the beach of Los Molinos A where 2 zones were differentiated: one located in the uppermost levels of the beach (*Orchestoidea tuberculata* and *Excirolana braziliensis*) and one over the mid-shore with the cirrolanid isopod *E. hirsuticauda* as the dominant species. While also reflective, this site differed from Maiquillahue and Codihue beaches in its finer sands and lower wave heights (Jaramillo & McLachlan 1993), which suggest a more benign swash climate. A 2-zone pattern with the same species as described above has also been observed in protected sandy beaches located at estuarine outlet areas of south-central Chile (Jaramillo 1987a, Jaramillo & González 1991).

Recently, classification and ordination techniques have been used to analyze the zonation patterns of the intertidal macroinfauna in various sandy beaches. Thus, 4 zones have been suggested for dissipative beaches in the USA (McLachlan 1990), South Africa (Bally 1983, Wendt & McLachlan 1985), Namibia (Donn & Cockcroft 1989) and south-central Chile (Jaramillo & González 1991), whereas 3 zones were suggested for a sandy beach located in northern Chile (Clarke & Peña 1988). The examination of kite diagrams and the results of the multivariate techniques in the present study suggest that in the intermediate and dissipative beaches the intertidal macroinfauna can be separated into 3 zones. The results of previous analyses were based upon the examination of a low number of sites, whereas ours are based upon a larger number representing a range of reflective to dissipative conditions. We believe that the more complete analysis undertaken here supersedes these previous studies.

The zonation scheme proposed by Dahl (1952) fits our data for the intermediate and dissipative beaches. Without the use of such multivariate techniques, Pichon (1967), Trevallion et al. (1970), Vohra (1971), Escofet et al. (1979) and McLachlan et al. (1981) among others, recognized similar zones in tropical and temperate waters. However, some differences were also found, the most important being those related to the presence of cirrolanid isopods in the upper zone (e.g. Pichon 1967, Jaramillo 1978, 1987b, Wendt & McLachlan 1985, Clarke & Peña 1988, De Ruyck et al. 1992), and bivalves in the middle zone (e.g. McLachlan 1980).

PCA of the physical data showed that stations could be ordered along an environmental gradient primarily related to the water content of the sediment in most beaches. The same was observed in CCA which showed that the ordination of stations and species for

most beaches is primarily accounted for by this physical factor. Down-shore variation in water content of the sand showed gradual changes across the intertidal zone below the drift lines; water content was less variable in beaches tending towards dissipative conditions. We could not differentiate the 4 physical zones proposed by Salvat (1964, 1967) (and later confirmed by Pollock & Hummon 1971) by observation or analysis. Other environmental variables also showed gradual changes across the intertidal zone of these beaches.

Body-size differences have been found in the down-shore distribution of several sandy beach organisms including gastropods (Edwards 1969), bivalves (Wade 1967, De Villiers 1975, McLachlan & Hanekom 1979, Bally 1983), hippid crabs (Efford 1965, Philip 1974, Haley 1982), amphipods (Craig 1973, Hager & Croker 1979) and cirrolanid isopods (Glynn et al. 1976, Dexter 1977). Zonation by size has been suggested to be related to factors such as beach morphology (Cubit 1968, Bowman & Dolan 1985). Differences in the intertidal distribution of different size classes of the most representative species in this study (*Orchestoidea tuberculata*, *Excirolana braziliensis*, *Excirolana hirsuticauda* and *Emerita analoga*) did not correspond to differences in beach state. Further analyses (long-term and laboratory studies) are needed before a conclusive statement can be presented concerning this aspect of intertidal variability.

Real zonation (like that observed in rocky shores) must be obvious, at least from kite diagrams, and for a zone to be valid it should harbour the centre of gravity of at least 1 species not typical of other zones. Arbitrary statistical separation of continuous or overlap regions does not constitute true zonation. In this study we have found evidence of true zonation reminiscent of the scheme proposed by Dahl (1952). Further, we have shown that an increasing number of faunal zones can be differentiated over a range of reflective to dissipative beach states. With the exception of the most reflective beaches, where only the top zone was present, neither the 2 zones found in a medium-sand reflective beach nor the 3 zones found in intermediate and dissipative beaches had sharp boundaries, a common feature of the intertidal sandy beach macroinfauna (McLachlan 1983). Despite the variability observed in the intermediate and dissipative beaches, we are confident of the presence of 3 zones, each with characteristic species. There is a faint tendency for the lowest zone to start to subdivide in the most dissipative states we investigated. It would be worth examining ultra-dissipative beaches to see whether this continues into eventual resolution of 4 zones as suggested by McLachlan (1990) for sandy beaches in Oregon, USA.

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